Notes on the genus Pandanus (Pandanaceae) in Western Australia

By Benjamin C. Stone*

Abstract

The genus *Pandanus* in Western Australia is known so far to occur only in the northern sector, in the Kimberley District, south to about 18° lat. Only one subgenus, Subg. *Pandanus*, is represented, but there are two distinct Sections, and possibly three, Sect. *Pandanus* (possibly), Sect. *Austrokeura* (herein raised to sectional rank from that of subsection), and Sect. *Semikeura*. The classification of species, especially in Sect. *Austrokeura*, is not as yet satisfactory. The occurrence of *P. spiralis* is documented, and a review of the species most similar to it included, resulting in some new synonyms and new combinations at infraspecific rank. Two new varieties (var. *flammeus*, var. *multimamnillatus*) are proposed. The variability of this species is discussed in relation to previously known and newly obtained specimens from both Western Australia and the Northern Territory. Three other species of subg. Pandanus, *P. darwinensis*, *P. oblatus* and *P. semiarmatus*, are also reported. Finally a new suite of collections of *P. aquaticus* (syn. *P. kimberleyanus*) is reported.

Introduction

Knowledge of *Pandanus* in Australia goes back a long way, to the exploratory activity of Robert Brown. Brown described only two species, *P. spiralis* and *P. pedunculatus*, in his "Prodromus Florae Novae Hollandiae et Insulae van Diemen" published in 1810. Brown's collections were studied recently by H. St. John, who published an account of these (St. John, 1968). According to St. John, Brown's collection no. *5799* was a mixture, and he selected as lectotype a portion of this gathering to typify *P. spiralis;* the material (one fruit phalange only) is illustrated in his fig. 267. Also assigned to the species but not considered to be part of the lectotype was a staminate specimen. This is correct, as all pandans are dioecious. Two phalanges were excluded from the three which made up the type materials of *P. spiralis*, and served as type (holotype) for St. John's new species *Pandanus brownii;* these phalanges are illustrated in his fig. 270. The lectotype of *P. spiralis* was obtained by Brown in the Gulf of Carpentaria on Allen Island, Wellesley Group (called by Brown "Island C"). The staminate inflorescence came from the same locality. The phalanges discriminated as *P. brownii* have an unknown provenence (except that they are assuredly from Brown's Australian travels). It cannot be assumed that they came from Allen Island, nor can it be proved that they did not.

Brown's second species was *P. pedunculatus;* this has good locality data, showing that it was collected at the north end of Great Sandy Island (now Fraser Island) off the E. coast of Queensland. The lectotype, also in the British Museum, was collected on 31 July 1802, and is given the number *5799A*. This species, which in the opinion of Domin was a variety of *Pandanus tectorius*, and in this writer's opinion is certainly part of the *P. tectorius* complex, has never been found in Western Australia; it is common however along the Queensland coast, especially on the offshore islands. It is known currently under a large number of different names, but that subject is dealt with elsewhere.

Further contributions to the knowledge of Australian Pandanaceae, especially *Pandanus*, have come from Martelli and more recently from St. John and Stone. Some of these contributions have dealt with collections

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made in the Northern Territory (St. John, 1962c), and several with Queensland material, but only one specifically refers to *Pandanus* in Western Australia; this is Part 2 of St. John's Revision of the Genus Pandanus (St. John, 1961a). In this paper St. John describes *P. kimberleyanus*, a species now assigned (Stone, 1974) to Section *Semikeura* Stone, and considered to be a synonym of, or at most but weakly distinct from, *P. aquaticus* F. Muell. St. John however also describes *P. convexus*, the type being a collection from Dillens Springs, now Dillon Springs, (*Fitzgerald 2394*). Other collections referred to the same species are a staminate inflorescence (*F. 2394*) from the same locality, and an unnumbered collection by *W. Hulse* from Escape Cliffs, Northern Territory, collected in 1874 or perhaps earlier. Martelli treated these as *P. spiralis* (Martelli, Proc. R. S. Qd. 45 (1933) 24.) St. John stated that *P. convexus* is related to *P. spiralis*, differing in its fewer carpels per phalange and a few other minor features.

In another relevant paper St. John (1962c) reports at length on a number of species, all but one described as new, from the Northern Territory. Although he states (p. 409) that *P. spiralis*, *P. delestangii*, *P. basedowii*, *P. whitei*, and *P. solms-laubachii* had been reported previously from the Northern Territory, he accepts only the records of *P. basedowii*. He therefore considers that *P. spiralis* is limited to its type locality, as mentioned above, which geographically is part of Queensland. Thus the key which St. John provides (p. 409) refers, with the sole exception of *P. basedowii*, only to his new species. It is difficult therefore to perceive the differences which would presumably serve to differentiate *P. spiralis* (sensu stricto) from the several highly similar species he describes.

There is of course no reason to suppose that the neat boundary lines which separate the Northern Territory from Western Australia and from Queensland are biogeographically meaningful. On the other hand, the scattered and local *Pandanus* populations of these regions which, away from the shoreline or the rivers, probably become highly disjunct, are a biogeographic feature of some importance.

Therefore, to discuss *Pandanus* in Western Australia, reference to what is known of the genus in the Northern Territory, and even in Queensland, has to be made. There is no evidence as yet to suggest that Western Australia harbours any unequivocal endemic species in this genus. Those few that have been described are at best weakly distinguished from their relatives and, as will be detailed below, recognition of a number of varieties seems to be the appropriate taxonomic solution at least until much more detailed studies, such as cytology, can be made.

The position of P. spiralis in the genus Pandanus

In Australia there may be found species representing the following three subgenera and six Sections (Subgenera 1 and 3 occurring only in Queensland):

1. Subg. LOPHOSTIGMA; Section *Maysops*
2. Subg. PANDANUS; Sections *Pandanus*, *Austrokeura*, *Semikeura*, and *Australibrassia*
3. Subg. ACROSTIGMA; Sect. *Acrostigma*.

Of these subgenera, only the second, i.e. Subg. *Pandanus*, occurs in Western Australia and in the Northern Territory. This subgenus, divided into several sections (Stone, 1974) is represented in both Western Australia and the Northern Territory by three Sections, viz. Sect. *Pandanus*, Sect. *Austrokeura* and Sect. *Semikeura*. The riverine species *P. aquaticus* ("P. Kimberleyanus") mentioned

above is the only representative of the typical subsection of this latter Section, while *P. basedowii* is the sole representative of Subsect. *Elaphrocarpus;* but this species has not been found so far outside the Northern Territory.

The character of Sect. *Austrokeura* itself is very distinct, and the chief distinguishing features are (1) rigid, very glaucous leaves, very prickly in juveniles, becoming semi-unarmed or nearly toothless, especially toward the apex, in adults: (2) stoloniferous habit: (3) presence of zonate epidermis and high numbers (i.e. density) of stomata on adaxial leaf surface, equalling the density on the undersurface or nearly so: (4) solitary cephalia. Probably other characters can be added to this list which help to distinguish this Section from Sect. *Pandanus*, in which *P. tectorius* (*P. pedunculatus*) is found.

Within *Pandanus*, Section *Austrokeura* is particularly characteristic of Australia (occurring elsewhere only in Papua, the contiguous southern part of West Irian and some immediately adjacent Moluccan islands). This group, founded on *P. solms-laubachii*, includes *P. spiralis*. Here it is raised to sectional rank.

Genus PANDANUS

Subgenus PANDANUS (sensu Stone, 1974b).

Sect. **Austrokeura** (B. C. Stone) B. C. Stone, *stat. nov.*

(*Pandanus* Sect. *Pandanus* Subsect. *Austrokeura* Stone, Bot. Jahrb. Syst. 94 : 517 (1974) Basionym).

(a) Series **Austrokeura.** Type: *Pandanus solms-laubachii.*

Phalanges laterally conspicuously sulcate, within the cephalium the phalanges interlocked by the groove-and-ridge system formed by these sulci. Phalanges various, from rotund to obovoid or suboblong. Mostly Queensland species, but some probably also in the Northern Territory.

(b) Series **Spirales** Stone, ser. nov.

Carpellis phalangiorum fere esulcatis; phalangibus rotundatis.

Type: *Pandanus spiralis* R. Br.

Mainly Western Australia and the Northern Territory.

This difference is not hard and fast but on the whole seems to reflect two real trends. Using this conception a group of 'forms' appears to cluster round *P. spiralis.* This group also shows these additional phalange characters: (1) broad, rounded shape of the phalange, and (2) the comparatively large number of carpels per phalange.

It becomes evident that the conspicuously ridged-and-grooved phalanges characteristic of Ser. *Austrokeura* are particularly common among Queensland species, becoming scarcer along an east-to-west gradient; while the smoother phalanges of the Ser. *Spirales* are most common in Western Australia and the Northern Territory, but scarce to absent in Queensland, especially eastern North Queensland. However, there are enough exceptions to suggest that there is possibly a "hybrid belt" of forms bridging the W. Queensland—E. Northern Territory populations, and that the ridge-and-groove character has "flowed" in a westerly direction.

The species which would be assigned to these groups are, if one simply followed the classification and species concept of St. John (which I do not accept) (Those marked * appear somewhat intermediate between the two series):

Ser. *Austrokeura: P. dammannii* Martelli, *P. arnhemensis* St. John, *P. citraceus* St. John, *P. cookii* Martelli, *P. angulatus* St. John, *P. australiensis* St. John, *P. truncatus* St. John, *P. ferrimontanus* St. John, *P. endeavourensis* St. John, *P. subinermis* St. John, **P. darwinensis* St. John, *P. orbicularis* St. John, *P. exarmatus* St. John, *P. phuriangulatus* St. John, *P. punctatus* St. John, *P. stolonifer* St. John, *P. latifructus* St. John, *P. papillosus* St. John, *P. mossmanicus* St. John, *P. radicifer* St. John, *P. kurandaensis* St. John, and *P. rivularis* St. John. Also, *P. brassii* Merr. & Perry of Papua belongs here, and probably *P. ananas* Martelli of Timor.

Ser. *Spirales: P. spiralis* R. Br., *P. integer* St. John, *P. convexus* St. John, **P. thermalis* St. John, *P. oblatus* St. John, *P. somersetensis* St. John, *P. semiarmatus* St. John.

Variability in P. spiralis

The very heading here underlines the assumption that forms the argument of this paper: that is, that *P. spiralis* is a variable species, not a local endemic restricted to Allen Island in the Gulf of Carpentaria. The proponent of this second view, St. John, naturally concludes that pandans which strongly resemble, but do not actually match, Brown's specimen (lectotype) of *P. spiralis*, must be assigned to other (usually undescribed) species.

However, the significant question is: wherein does the variability lie? Brown's type specimen being fragmentary, there is really only the fruit to consider, and this is represented only by two phalanges—hardly enough to enable one to form any notion of variability in an individual, let alone a species.

Study of a considerable amount of material of *Pandanus* has shown that there are many kinds of variation to be found among fruits or phalanges from the same plant, and from different plants of the same species. This has been dealt with at length in previous reports (Stone, 1967a, 1967b, 1976) and need not be repeated here. Suffice it to say that some kinds of variation obviously are unsuitable for discriminating species; juvenile characters, features of unfertilized fruits or unripe material, shrinkage in drying, etc., all these must be eliminated. Such variability as remains is then worth serious consideration. However, structures other than fruits must be examined as well; foliage differences do exist between species, and even staminate characters may be of use. Among the Australian species, the whole of Sect. *Austrokeura* is however characterized by a very stereotyped leaf form, and so far, no good characters sufficient to differentiate species have been found in the leaves. So, also, the staminate inflorescences: they are inherently exceedingly similar. If differences exist, they are liable to be subtle, statistical, and ephemeral. Of necessity we fall back on fruits as taxonomic markers. On this basis, almost exclusively, St. John has proposed more than two dozen species in Sect. *Austrokeura*. In this paper however attention will be focussed on those which I have assigned to Ser. *Spirales* and to the apparently intermediate *P. darwinensis;* and it is the intent here to show how and why I prefer to regard *P. spiralis* as a complex species which, for convenience, as much as to facilitate discussion and study, is deemed to consist of several subordinate taxa here called varieties. Some of these may prove to be subspecies, in the stricter biological sense, but others may be ephemeral taxa; hence the decision to use the category *varietas* (see Stone, 1976).

P. spiralis, its varieties and related species

The main variations in phalanges of *P. spiralis* and its nearest relatives involve the following characters:

(1) Number of carpels per phalange (see Stone, 1967)

(2) Size of phalange, particularly length

(3) "Rotundity" versus "complanation" of the phalange apex

(4) Relative convexity of each component carpel apex

(5) Presence or absence of lateral sulci (in extreme cases forming a dense series of longitudinal ridges and grooves)

(6) Size of stigmas

Chiefly using these characters, St. John has discriminated three species (*P. convexus*, *P. integer*, *P. thermalis*), which were considered as close relatives of *P. spiralis*, but which here are regarded as subordinate taxa of that species. St. John in his original diagnoses often indicates a "closest relative" but this seems to be based chiefly on the position of such taxa in his unpublished keys to species. These species, and seven others which on morphological grounds and geographical distribution are thought also to be implicated, with the indicated 'closest relative' according to St. John, are:

P. convexus St. John, 1961: "Closest Relative": *P. spiralis*

P. integer St. John, 1962: "Closest Relative": *P. convexus*

P. thermalis St. John, 1962: "Closest Relative": *P. latifructus*

P. latifructus St. John, 1962: "Closest Relative": *P. medialinermis*

P. medialinermis St. John, 1962: "Closest Relative": *P. somersetensis*

P. somersetensis St. John, 1961: "Closest Relative": Not indicated

P. darwinensis St. John, 1962: "Closest Relative": *P. whitei*

P. arnhemensis St. John, 1962: "Closest Relative": *P. truncatus*

P. truncatus St. John, 1961: "Closest Relative": *P. brookei*

From this sequence it may be seen that a series of forms may be deduced, *convexus—spiralis—integer*; then another series, *thermalis—latifructus—medialinermis—somersetensis;* then a pair, *darwinensis—whitei;* and then another short series, *arnhemensis—truncatus—brookei*. It is a standard feature of the taxonomic papers of Dr. St. John to state such a "closest relative", but it is disputable whether it is correct to assume that a species has always and only one close relative. In any case the sequences noted are instructive. If reference is made (prev. page) to the species listed under each of the newly proposed Series, it is seen that the species of the first sequence (*convexus—spiralis—integer*) have phalanges with smooth faces and no ridge-and-groove system; the species of the second sequence (*thermalis—latifructus—medialinermis—somersetensis*) are mixed with respect to the ridge-and-groove character, *somersetensis* and *thermalis* lacking the system (*thermalis* possesses perhaps a very weak expression of this character), while *latifructus* and *medialinermis* show the character strongly developed; *darwinensis* and *whitei* both show the character; and in the last sequence, *arnhemensis* and *truncatus* strongly show the ridge-and-groove system, but *brookei* lacks it entirely.

To these facts must be added the point that as far as can be determined, *P. brookei* is extremely similar (= closely related?) to *P. somersetensis*, a relationship not indicated by St. John. I do not consider that *P. truncatus* should be considered as a close relative of *P. brookei*, nor do I accept *P. somersetensis* as a close relative of *P. medialinermis*. (The latter in fact is most likely a synonym of *P. dammannii* Warb.). Furthermore I would consider *P. truncatus* as a synonym of *P. whitei* Martelli; this taxonomic interpretation would then link the isolated pair, *darwinensis-whitei*, with the final sequence, where we may substitute *whitei* for *truncatus*, all these species then linking into a single sequence *darwinensis—whitei—arnhemensis*.

On the basis of the ridge-and-groove character, *P. thermalis* links more readily with the *spiralis* group, and we may postulate the sequence *convexus—spiralis—integer—thermalis*.

Having thus removed both *P. thermalis* and *P. somersetensis* from the second sequence, and added *P. dammannii* (to replace its synonym *P. medial-inermis*), only a pair remains: *latifructus—dammannii*. However, it is now evident that *P. dammannii* is similar to *P. arnhemensis;* hence we may form a linkage with the last sequence, which would now be *darwinensis—whitei—arnhemensis—dammannii—latifructus*.

Reviewing the situation we now see only two sequences:

(1) *P. convexus—P. spiralis—P. integer—P. thermalis;*

and

(2) *P. darwinensis—P. whitei—P. arnhemensis—P. dammannii—P. latifructus*.

The first of these corresponds to Ser. Spirales, the second to Ser. Austrokeura. The distinctiveness of the two Series is partly threatened by *P. darwinensis*, which has a strong ridge-and-groove system, but has large, rotund phalanges with a fairly high (11–13) number of carpels per phalange, approaching *P. spiralis;* and by *P. thermalis*, which has a weakly developed ridge-and-groove system but otherwise rather smooth phalange faces, large rotund phalanges, and a moderate number of carpels per phalange (9–11), thus also approaching *P. spiralis*.

In other words, it is possible to view *P. thermalis* and *P. darwinensis* as a linked pair; to do so would necessarily link the two sequences, or Series, as indicated above.

Does this not then make ineffectual the distinction between Series *Spirales* and Ser. *Austrokeura*?

I do not think so, and this is because the distributional and geographic data support the distinction. If the two Series are not completely separate, it is because there is a distributional continuity across the northern tropical region of Australia. It remains a useful distinction, although it may only be an expendable taxonomic tool, as long as a multiplicity of species in these Series is accepted. It affords recognition to the probability that species characters (better to say phalange characters) are subject to reassortment, and that the ridge-and-groove character may be incorporated through inheritance as a randomly assorting character. If this be so then one may postulate that forms such as *P. darwinensis* and *P. thermalis* may be hybrids of a type approximating to the expression: "spiralis" type × "whitei" type, which in geographic terms is to say "Northern Territory" × "Queensland." It is what might be expected at the interface of two distributional areas, whence further recombinations might produce, toward the western portion, forms such as *P. thermalis*.

But it is not necessary to assume that *P. darwinensis*, etc., are species, and if these speculations as to origin are anywhere near the historical reality, then other taxonomic dispositions of such 'species' might be preferred. Perhaps the designation *P.* × *darwinensis* would be suitable. However, in the absence of any proofs of hybridization, this designation might be prejudicial. In any case, a suspicion exists (based on other, non-Australian *Pandanus* species) that asexual forms of reproduction may occur. Of course, clonal reproduction by stolons is known to exist in *P. spiralis* and several other Australian species, but it is also possible that apomixis may occur. If so, then the possibility of a taxonomic situation resembling that found in such genera as *Taraxacum*, *Hieracium*, and *Rubus* might exist, which if it did occur would profoundly affect all the taxa enumerated here.

Tentative Key to species and varieties

1. Phalanges slender oblanceoloid, small (mostly 4–5 cm long), usually 1-celled or sometimes 2–3-celled. Cephalia when ripe subglobose-ovoid. Staminal phalanges with racemosely disposed filaments, these comparatively few and wide-spaced on the column. Habitat along streams .... Section SEMIKEURA
(One species, **P. aquaticus**)

1. Phalanges obovoid to subglobose-rotund, often large to massive, always of more than 4 cells and often with 7–22 cells (or more). Cephalia when ripe ellipsoid to subglobose. Staminal phalanges with numerous crowded racemosely disposed filaments. Habitats various .... Section AUSTROKEURA

2. Phalanges with several to many supernumerary ridges and grooves besides the normal intercarpellary sulci, in intact cephalia interlocking adjacent phalanges (mortise-tenon effect). Phalanges usually large (7 cm +), equidiametric, rotund, or somewhat laterally compressed.

3. Phalanges about 7·5 x 6—7·5 cm, massive, rotund, convex, carpel tips convex .... 4. **P. darwinensis** var. **darwinensis**

3. Phalanges about 5 x 6–7 cm, convex, the carpel tips very low-convex to flattened, whole phalange somewhat laterally compressed .... 4. **P. darwinensis** var. **latifructus**

2. Phalanges with no, or very few, supernumerary ridges and grooves, the faces comparatively smooth, broken only by the intercarpellary sulci. Phalanges medium to massive, rotund and equidiametric or somewhat laterally compressed.

4. Phalanges mostly equidiametric, rotund. Carpels rather numerous to numerous (to 20 or more) within the phalange.

5. Carpels with sharply acute convex tips; carpel number high (15–23) .... 1. **P. spiralis** var. **multimammillatus**

5. Carpels tips low convex to nearly flat.

6. Phalange apex slightly concave, the carpel tips flat; phalanges tending toward extreme shallowness. .... 1. **P. spiralis** var. **flammeus**

6. Phalange apex rotund, low convex, or nearly flat, but not concave; individual carpel tips usually slightly convex.

7. Phalanges multicarpellate (carpels 12–24), carpels broad.

8. Phalange apex dome-shaped, carpel tips little prominent. Lateral faces of phalange smooth; carpel number high (up to 24) .... 1. **P. spiralis** var. **spiralis**

8. Phalange apex dome-shaped but the individual carpel tips somewhat obtruding; lateral faces of phalange with a few supernumerary ridges and grooves; carpel number moderate (9–11, perhaps more) .... 1. **P. spiralis** var. **thermalis**

7. Phalanges with mostly 5–15 carpels .... 1. **P. spiralis** var. **convexus**

4. Phalanges mostly subcompressed to compressed laterally, not rotund. Carpels mostly 5–12 per phalange.

9. Phalanges about 6·5—7 x 5 cm .... 2. **P. oblatus**

9. Phalanges about 5·5 x 5 cm .... 3. **P. semiarmatus**

1. Subgenus **Pandanus**, Section **Austrokeura** (Stone) B. C. Stone, *supra*. (1) Series *Spirales* Stone.

1. **Pandanus spiralis** R. Br. (Fig. 1).

var. **spiralis.** Phalanges broad, rotund, about 6 x 7–8 cm, multicarpellate, with as many as 19–23 carpels per phalange; apical sutures shallow, individual carpel apices very low convex, hardly raised above the general dome-like phalange apex; lateral sutures few, shallow, short; stigmas 1·5–2 mm wide.

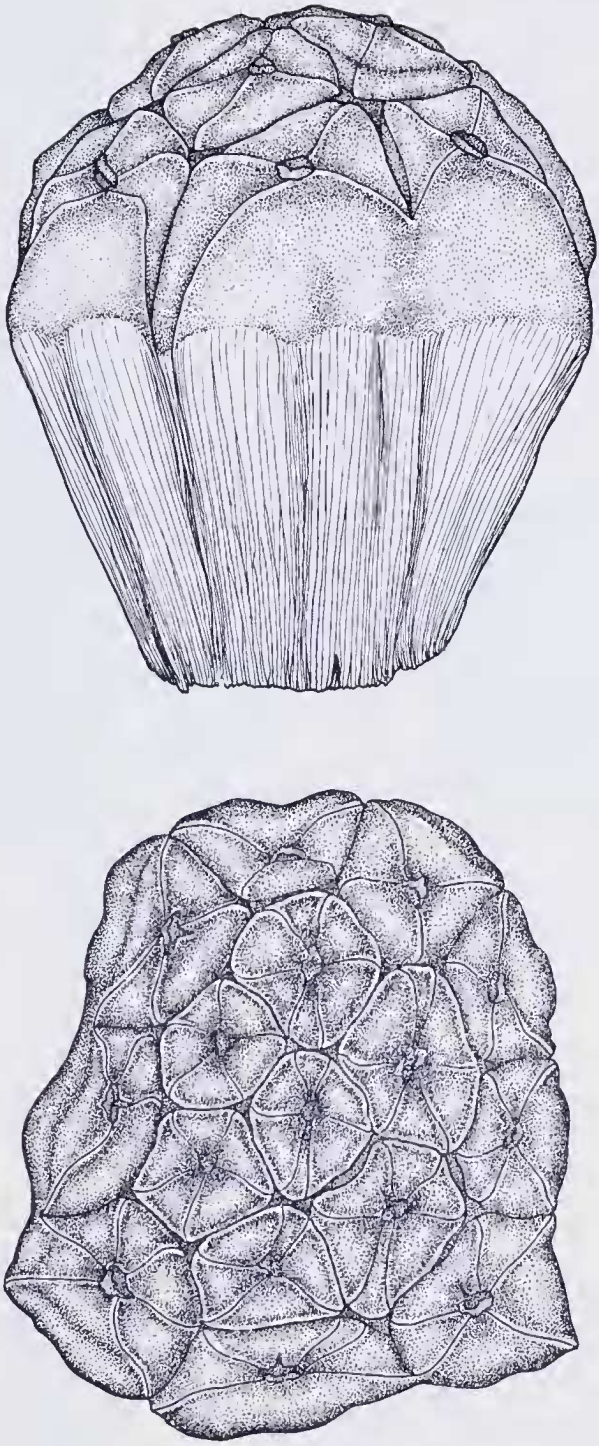

Figure 1—Phalange (top and profile) of *Pandanus spiralis* var. *spiralis*. (From ASG s.n. 8/1975, Drysdale River N.P.).

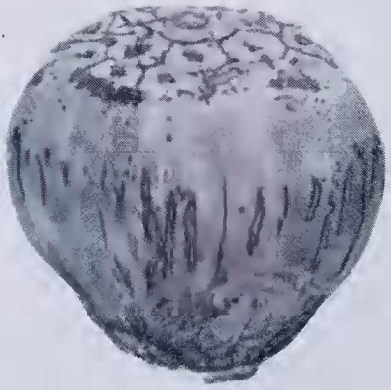

Figure 2—*Pandanus spiralis* var. *convexus*. Above: habit and habitat; below; a phalange. (From ASG 12634).

New collections: WESTERN AUSTRALIA: Drysdale River National Park, August 1975 *A. S. George* s. n. (PERTH). (Phalanges precisely as in the R. Brown collection); Prince, Regent River Reserve, 19 August 1974, *K. F. Kenneally* s.n. (PERTH).

var. **convexus** (St. John) B. C. Stone, stat. nov. (Fig. 2).

Basionym: *P. convexus* St. John, Pacif. Sci. 15 (1961) 183, f. 10.

Type: W. V. Fitzgerald 2394, Dillens Springs, Western Australia (NSW).

Syn. *P. integer* St. John, Pacif. Sci. 16 (1962) 414, f. 142. *Type: R. A. Perry* 2630, 20 mi. S. of Laguna Sta., N.T. in Herb. BRI.

Phalanges broad, rotund, 5–6 x 5–7 cm, with about 6–10 carpels per phalange: apical sutures shallow, carpel tips flattened; lateral sutures none or few; stigmas 3–5 mm long.

New collections: WESTERN AUSTRALIA: Prince Regent River Reserve, W. Kimberley; residual pool in sandstone outcrop; common in this area; 14 August, 1974 *K. F. Kenneally* 2041 (PERTH); Same locale, Fern Gully, fringing forest along creek, rocky sandy-substrate; tree 10 m tall; fruit top orange-brown, base red; 25 August 1974, *A. S. George* 12634 (PERTH); Drysdale National Park, August 1975, *K. F. Kenneally* 3080, 4348, 4518 (PERTH).

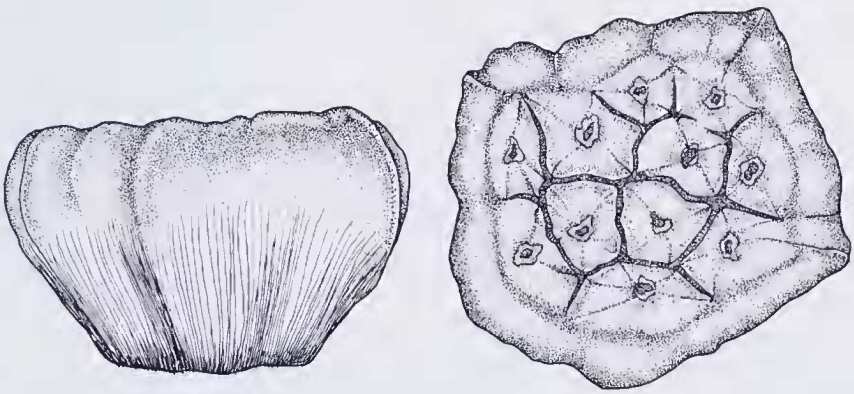

Figure 3—*Pandanus spiralis* var. *flammeus*. Profile and top view of phalange (from holotype).

var. **flammeus** B. C. Stone, var. nov. (Figures 3, 4). *Holotype: K. F. Kenneally* 5680, Logues Springs, W.A. in Herb. PERTH. Isotype in KLU.

Phalanges 6–12 carpidiatae, plerumque 3·5—4·5 cm longae, 5—6·5 cm latae, apicaliter complanato-depressae, superficie distali vadose depresso-concava, suturis pervadosis tenuis irregulariter suberosis, suturis lateralibus raris vel carentibus; pericarpio aurantiaco-ruhro.

WESTERN AUSTRALIA: Logues Spring (18° 25′ S, 123° 05′ E) south-east of Broome; screwpine to 5 m, stems thin, foliage glaucous, fruits scarlet with 16 'drupes' (i.e. phalanges); restricted to small narrow gorge containing a series of water holes fed by a spring; soil rocky, with fine, white, dusty clays boggy during wet (season); 15 August 1976. *K. F. Kenneally* 5680 (PERTH).

The slender leaves, those of adults only 4–5 cm wide (the juvenile leaves, as usual, prickly, and the adult leaves almost unarmed), the small cephalium about 13 x 13 cm., and small number of phalanges borne on the cephalium, may be additional characters of this variety.

The carpel number per phalange shows two peaks; analysis of the cephalium gives the following results:

1 phalange with 6 carpels; 2 phalanges with 7 carpels; 4 phalanges with 8 carpels; 2 phalanges with 9 carpels; 2 phalanges with 10 carpels; 3 phalanges with 11 carpels; 1 phalange with 12 carpels.

Figure 4—*Pandanus spiralis* var. *flammeus*. Above: habit and habitat; below; cephalium. (From type locality and holotype).

The stigmas are small and obscure, difficult to make out in the ripe phalanges; most are 1–2 mm long. Several phalanges exhibit abnormal, peripheral, dwarf or undeveloped, partly free and convex supernumerary carpels.

var. **multimammillatus** B. C. Stone, var. nov. (Figure 5). *Holotype: A. S. George* 13380, (PERTH), W. of Cape Londonderry, W.A. Isotype in KLU.

Phalanges 15–23-carpidiatae, rotundae, convexae, 5–6 x 5–6·5 cm, fere subglobosae; carpellis subaequalibus, apice alte pyramidato-convexibus, angulatis, pyramidis usque ad 7–9 mm altis, stigmatibus obliquis atrobrunneis 2–3 mm longis. Mesocarpium in basi fibris brevissimis. Epicarpium pauci-canaliculatum in medio.

WESTERN AUSTRALIA: Far north west coast, West of Cape Londonderry, tree to 5 m tall in black loam in woodland with dense grass understorey, fruit orange-red, 5 August 1975, *A. S. George* 13380 (PERTH).

In its multicarpellate phalanges of rotund form this variety approaches var. *spiralis*, but the smaller phalange size, and especially the steeply pyramidal carpel tips with obvious slanted stigmas give this variety clearcut distinguishing features. The apical sutures are often dark-tissued (scars) and the phalange sides are fairly smooth, a few shallow ridges and grooves developing unequally in some but not all phalanges. The leaves seem to have no distinguishing features, the adult leaves apparently (as is normal) armed remotely along the margins proximally but the leaf apices minutely and sparsely prickly or for long stretches of margin or even the entire apex unarmed.

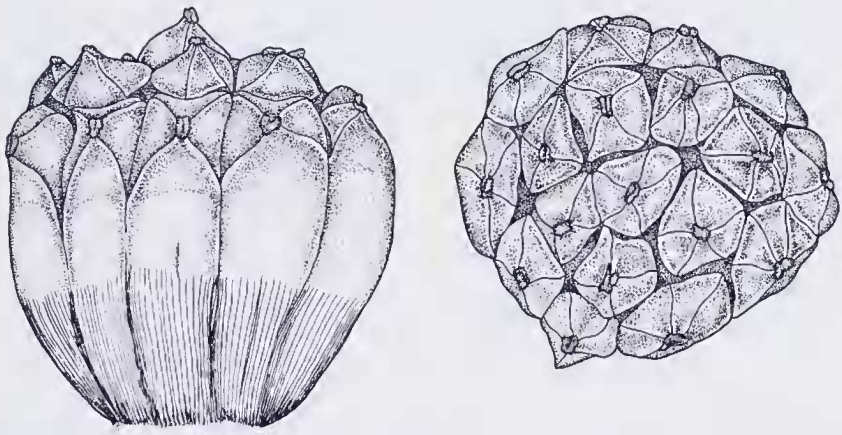

Figure 5—*Pandanus spiralis* var. *multimammillatus*. Profile and top view of phalange (from holotype, ASG 13380).

var. **thermalis** (St. John) B. C. Stone, stat. nov.

Basionym: *P. thermalis* St. John, Pacif. Sci. 16 (1962) 423, f. 148.

Type: S. T. Blake 16433, Hot Springs, Douglas R., N.T. in Herb. BRI.

Phalanges broad, rotund. 7–7·5 x 6·8–8·5 cm, with about 9–11 earpels; phalange apex dome-shaped, earpel tips nearly flat, apical sutures shallow, lateral sutures well marked and deep but comprising only, or mainly, intercarpellar sutures; stigmas 3·5–5 mm wide.

New collections: WESTERN AUSTRALIA: Drysdale River National Park, 14 49′ S, 126 49′ E; tree to 8 m, fruit red, aerial rootlets present; in sand; woodland; 10 August 1975, *A. S. George* 13677 (PERTH) (Carpel tips oblique subdepressed; lateral faces with grooves); Prince Regent River Reserve, Aug. 1974, *K. F. Kenneally* s.n. (PERTH); Drysdale River National Park, 15 02′ S, 126 49′ E, Carson Escarpment, Drysdale River, seepage area at base of sandstone hill, tree 8 m, fruit pale orange-brown, red at base, 16 August 1975, *A. S. George* 13898 (PERTH).

2. **Pandanus** (Austrokeura) **oblatus** St. John ? (= *P. somersetensis* St. John) (Figure 6A).

WESTERN AUSTRALIA; Drysdale River National Park, 15° 02′ S, 126° 40′ E, Worriga Gorge, tree to 8 m tall, with aerial rootlets, fruit red, in damp black loam by creek in grassy woodland, 20 August 1975, *A. S. George* 14084 (PERTH).

In its phalanges this collection shows a very strong resemblance to *Pandanus oblatus* St. John (Pacif. Sci. 15 (1961) 569, f. 27, 28), described from specimens collected by *L. J. Brass* in the Iron Range, Cape York, Queensland, at 20 m alt. (no. 19312 Type, in BRI), still the only known collection. However, the leaves in that species are described as fully armed, with the margins denticulate from base to apex. Almost certainly, this indicates that the leaf collected by Brass was from a vigorous juvenile individual, or perhaps a tiller shoot, but this cannot be proven. In the *George* specimen cited above, the leaves are almost unarmed, i.e. perfectly normal for Sect. Austrokeura *adult* leaves. In addition the phalanges of the *George* specimen are slightly shorter. Thus I refrain from actually certifying an identity. There is no easy alternative identification and indeed the *George* collection is unique among the Western Australian speci-

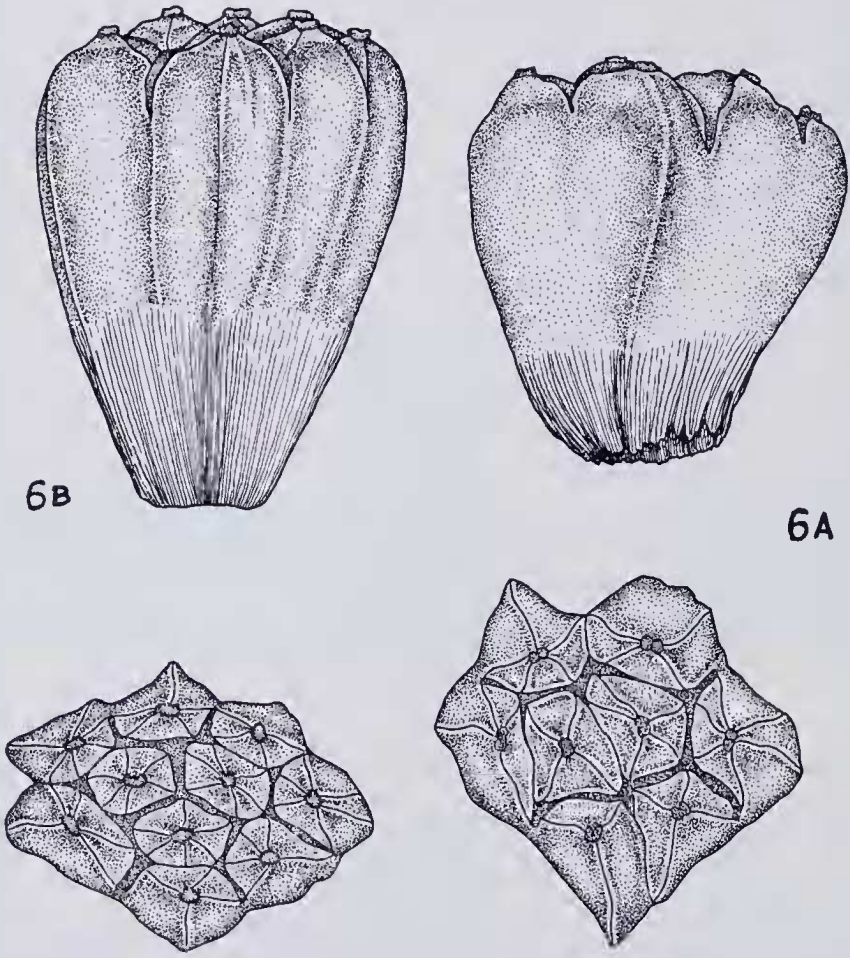

Figure 6—Profiles and top views of phalanges. At right, upper and lower; *Pandanus oblatus* (from ASG 14084). At left, upper and lower; *Pandanus semiarmatus* (from KFK 4514).

mens which I have seen. It may be a new species, but in the welter of already published names, and the evident redundancy (and synonymy) of species names in this deceptive and difficult group, it is not deemed appropriate to make a decision at this stage. It cannot readily be included within the (now broadened) concept of *P. spiralis* because of the very small and paucilocular phalanges (less than 5 cm long), although because of the smooth phalange faces it would appear to correspond with this species insofar as being placed in Ser. *Spirales*. It is possibly a very depauperate form of *P. spiralis* var. *convexus*, or closely related to it. It is obviously a form which is at the extreme border of the concept of one species or another.

I consider *P. somersetensis* St. John (Pacif. Sci. 15 (1961) 570, f. 29) as identical with *P. oblatus*.

3. **Pandanus semiarmatus** St. John, Pacif. Sci. 16 (1962) 421, f. 147. (Figure 6B).

Type: Blake 19694 (BRI), from Koolpinyah, N.T.

WESTERN AUSTRALIA: Drysdale River National Park, Site B3, 127° 12′ E, 15° 17′ S, on edge of remnant pool of Johnson Creek, very common, 9 August 1975, *K. F. Kenneally* 4138 (PERTH); Same locale, 127° 05′ E, 14° 47′ S, side of dry creekbed, commonly around remnant pools, 10 August 1975, *Kenneally* 4174 (PERTH); Same locale, Site B2, 126° 55′ E, 14° 49′ S, beside creek, 14 August 1975, *Kenneally* 4318 (PERTH); Same locale, Site C3, 126° 54′ E, 14° 43′ S, common along edge of creek and by remnant pools, 20 August 1975, *Kenneally* 4514 (PERTH); Same locale, 126° 44′ E, 15° 16′ S, in sand in woodland, tree 6 m tall, foliage slightly bluish, fruit green, 3 August 1975, *A. S. George* 13202 (PERTH).

All these specimens accord well with each other, and with the diagnosis and illustration of *P. semiarmatus*, though the last cited specimen (*George 13202*), being of a very immature fruit, is less surely placed. These records make this species an addition to the Western Australian flora from their previous local distribution in the Northern Territory (Koolpinyah just E of Darwin), but the distance is not excessive and no doubt this species has an intermittent but probably even wider distribution along the north Australian coast and hinterland.

St. John relates this species to *P. somersetensis* of Queensland. The Blake collection (the type) was until now the only known collection.

P. semiarmatus is clearly a member of Sect. *Austrokeura*, as shown by its unarmed leaf apices and the massive endocarps. It is very close to *P. spiralis* and could well be considered a variety of it, a disposition which may be preferred after further studies in this group; yet it has a certain distinctiveness, in the slightly compressed phalanges and their very smooth lateral faces. The character which suggested the epithet *semiarmatus* (unequal presence of prickles on the leaf margins—one margin often unarmed) is by no means a specific character and should carry no weight at all, for although it is odd it varies from tree to tree and has also been noticed in cultivated plants of the (hardly closely related) *P. tectorius*.

(2) Series *Austrokeura*

4. **Pandanus darwinensis** St. John, Pacif. Sci. 16 (1962) 417, f. 144.

Type: Allen in 1927, near Darwin, N. T. (BRI).

var. **darwinensis** (Figures 7, 8).

Phalanges massive, rotund, with thick epicarp, very short basal mesocarp; carpel tips convex, whole apex of phalange convex; apical sutures obvious; lateral sutures obvious; phalange sides (carpel sides) with longitudinal ridges and grooves; phalanges about 7·5 x 6–7·5 cm; carpels 11–13 and subequal; stigmas 3–3·5 mm long.

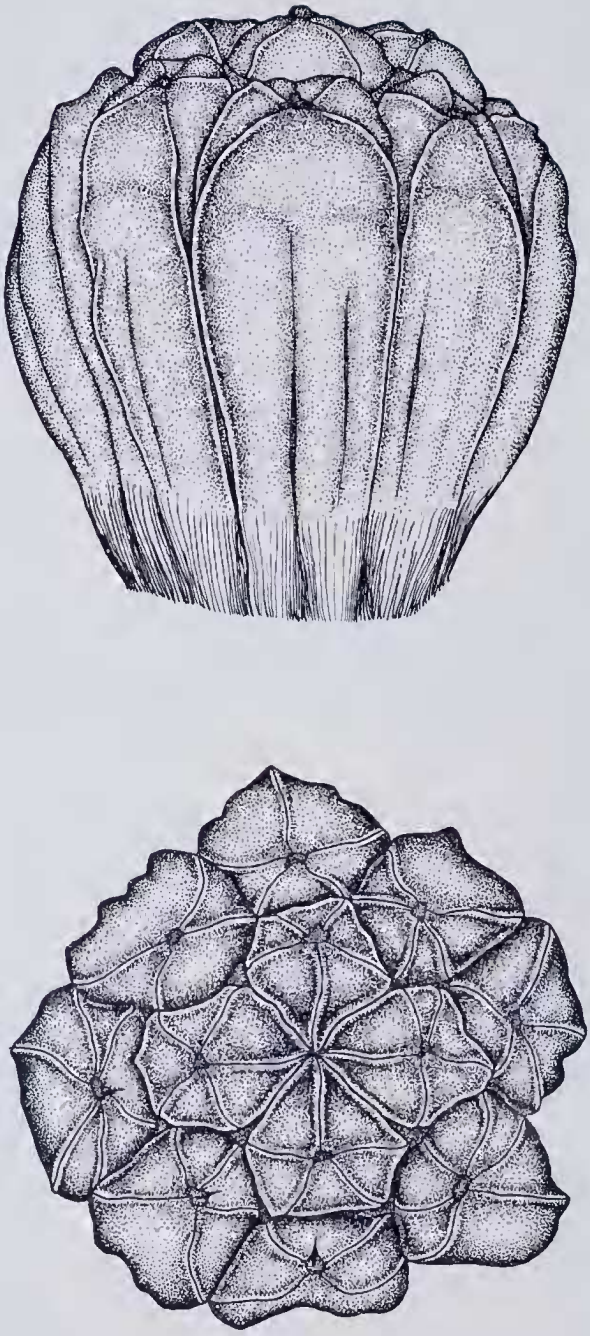

Figure 7—*Pandanus darwinensis*. Phalange, profile and top view. (From BCS 10650).

New collections: WESTERN AUSTRALIA: Prince Regent River Reserve, 19 August 1974, *A. S. George* 12411 (PERTH); Same locale, 3 August 1974, *K. F. Kenneally* s.n. (PERTH); Drysdale River National Park, August 1975, *A. S. George* 13315, 13457 (PERTH). NORTHERN TERRITORY: Dashwood Creek, near Darwin, 3 Sept 1971, *B. C. Stone* 10650, 10651 (KLU).

In relating *P. darwinensis* to *P. spiralis*, I acknowledge that the character of lateral longitudinal ridge-and-groove systems of the phalanges can occur in the species. It appears to me that this character is derived from hybridization with related species in Ser. *Austrokeura* to the east, especially *P. whitei* and its relatives. Indeed, *P. darwinensis* may be in part a recombination of characters from *P. spiralis* and *P. whitei*, the massive size and rotundity of the phalanges from the first, the ridge-and-groove system from the second; of course this is sheer speculation. It is also true that the incidence of the character—which affords a kind of mortise and tenon interlocking (not really effective perhaps)—may vary somewhat within a cephalium, and not every phalange is equally affected.

It is a very obvious character, yet its significance, as well as its heredity, is not well understood.

var. **latifructus** (St. John) B. C. Stone, stat. nov.

Basionym: *P. latifructus* St. John, Pacif. Sci. 16 (1962) 420, f. 146.

Figure 8—*Pandanus darwinensis*. Habit, showing branch, leaves and cephalium. From ASG 12411, Prince Regent River Reserve.

Type: H. St. John 24225, 22 mi. S. of Darwin, N.T. in BISH.

Phalanges broad, rotund, about 5 x 6–7 cm, with 12–20 carpels per phalange, apex of phalange dome-shaped, carpel tips very low convex to flattened but apical sutures deep and rather wide; lateral sutures deep, numerous; stigmas 1–2 mm.

Very similar to var. *arnhemensis*, also to var. *darwinensis*.

New collections: WESTERN AUSTRALIA; West of Cape Londonderry, 5 August 1975, *A. S. George* 13375 (PERTH).

II. **Pandanus** Subg. **Pandanus** Sect. **Semikeura** B. C. Stone, Contrib. Herb. Austral. No. 5, (1974) 42.

This small, characteristic section is composed of two subsections; of these only one so far is known from Western Australia. The other, subsect. *Elaplurocarpus* B. C. Stone, is monotypic, and its single species, *P. basedowii* C. H. Wright, is known to date only from Arnhem Land, Northern Territory.

Subsect. *Semikeura*

Type species: *P. delestangii* Martelli, a synonym of *P. aquaticus* F. Muell.

This subsection, which I consider monotypic, ranges right across north Australia from Queensland to Western Australia. Although five species have been described in this group, there are no useful distinctive characters, although one form, named *P. kimberleyanus* St. John, has fruits of which the drupes are rather short for what seems to be the average. With Blake (1954, 130, pl. 7, f. 3) I consider *P. aquaticus* the correct name of the species, and although slightly variable there seems no justification to recognize additional species.

Some new collections have recently been made, cited here.

5. **Pandanus aquaticus** F. Muell. in Hook. J. Bot. Kew Gard. Misc. 8(1856) 329, nomen provisorium; Fragm. Phyto. Aust. 5 (1865) 40 (validation); Stone, Contrib. Herb. Austral. no. 5 (1974) 42.

Syn. *P. kimberleyanus* St. John, Pacif. Sci. 15 (1961) 180, f. 9.

Type: Fitzgerald 2395, Fitzroy River, Kimberley, W.A. (NSW).

WESTERN AUSTRALIA: Drysdale National Park, 15° 02′ S, 126° 55′ E, common on river banks, trees 5–6 m tall, rather slender, aerial rootlets present, fruit fallen, 6 August 1975, *A. S. George* 13486 (PERTH); Same locale, Carson River, 14° 49′ S, 126° 49′ E, 11 August 1975, *A. S. George* 13705 (PERTH); Same locale, Site C2, 15° 03′ S, 126° 44′ E, very common, 17 August 1975, *K. F. Kenneally* 4388 (PERTH).

Of these specimens the drupes of *13705* are like those of the form called *P. kimberleyanus*, but not quite so blunt; while in *4388* the drupes are more slender, as in *P. delestangii*.

Addendum

There is in the W.A. Herbarium (PERTH) a collection made by *E. M. Bennett*, no. 1815, labelled "Pandanus tectorius" and consisting of some phalanges of what is clearly a member of the *Austrokeura* group; however locality data are lacking (collected 20/5/1967) and I refrain from describing it. It is almost certainly an undescribed new variety of *Pandanus spiralis*.

Acknowledgements

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study of Australian Pandans. The photographs were provided by them, except for the isolated phalange (A. S. G. 12634) which was photographed for me by the Rijksherbarium, Leiden, and forwarded to me by Mr. A. K. Groenewegen of that institution. The line drawings herein are by Encik Rosali of the Dept. of Botany, University of Malaya.

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